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MILTON WHITNEY, *Chief.*

SOME FACTORS INFLUENCING SOIL FERTILITY.

BY

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LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Soils,
Washington, D. C., January 11, 1907.

Sir: I have the honor to transmit the manuscript of a paper entitled "Some Factors Influencing Soil Fertility," by Dr. Oswald Schreiner, in charge of fertility investigations, and Howard S. Reed, of this Bureau.

In accordance with your suggestion this paper has been gone over carefully with Assistant Secretary Hays, who authorizes me to state that he concurs in my recommendation for its publication. I recommend, therefore, that this article be published as Bulletin No. 40 of the Bureau of Soils.

Respectfully,

Milton Whitney,
Chief of Bureau.

Hon. James Wilson,
Secretary of Agriculture.

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SOME FACTORS INFLUENCING SOIL FERTILITY.

THE TOXIC PROPERTIES OF UNPRODUCTIVE SOILS.

A number of typically unproductive soils from different parts of the United States have been under study in the laboratories of the Bureau of Soils for several years, and some of their properties are now understood. It has been demonstrated that many soils are unproductive not because proper nutrients are lacking, but because they contain substances actually deleterious to plant growth.[a]

Some of the experiments which establish the existence of such deleterious substances are briefly given in the following paragraphs.

An extract of an unproductive soil, though containing nutrient substances, is often a poorer medium for the growth of plants than distilled water, although the latter contains no plant food whatever. Wheat seedlings will grow about three weeks in good distilled water, but various experiments described in the publications just cited show that such seedlings, when grown in the extract of an unproductive soil, give a much poorer growth in both top and root, the latter being usually much stunted in development, and the plants often die within two weeks. Such an experiment with a poor soil extract is shown in Plate I, figure 1. The good growth of both top and roots in pure distilled water is shown by No. 1 in the figure. No. 2 represents the plants grown in the extract from the poor soil, made by treating one part of soil with five parts of distilled water, and filtering through a porous clay Pasteur-Chamberland filter tube. The plants obtained are far inferior to those grown in distilled water in both top and root development, although the extract contains plant nutrients and the distilled water contains none. The roots are short, coarse, discolored, and seldom branch. The tips of the roots are always much stunted and often blackened.

Kellermann and Robinson[b] have also shown that soil bacteria are markedly affected by soil conditions in the same manner as the wheat

[a] A great deal of evidence on this point has been already presented in Bulletins 28 and 36 of this Bureau, and a general presentation of these results in Farmers' Bulletin 257 of the United States Department of Agriculture.

[b] Bul. 100, Part VIII, p. 8, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1906.

seedlings. They found that the sterile aqueous extract of a soil which did not respond to inoculation with *Pseudomonas radicicola* likewise proved to be a very poor culture medium for the development of the bacteria. After treating the soil with lime, however, the deleterious conditions were eliminated and the extract from the soil proved an excellent medium for bacterial growth, resembling in this respect the results obtained with higher plants by liming. These facts show very clearly that soil conditions play as important a part in the development of the proper bacterial flora in soils as in the growth of the higher plants.

When such a poor soil extract, exhibiting toxic properties toward plant development, is treated with insoluble finely divided bodies which are good absorbing agents, a marked increase in the growth of both tops and roots is noticed in the extract, which becomes, in fact, a good medium for plant growth. This is strikingly shown by the plants No. 3 in Plate I, figure 1, where the toxic property of the soil extract which hindered plant growth, as shown in No. 2, was removed by adding a small amount of carbon black, shaking, and filtering the carbon black off again. The carbon black contains no nutritive substances whatever, as it is obtained by burning natural gas and collecting the separated carbon on cool surfaces. The growth in this treated extract is now even better, as it should be, than in the distilled water, which contains no nutrients whatever. Nos. 2 and 3, however, contain the same amounts of nutrient salts, and the conclusion is obvious that the retarded growth in the original soil extract was due to the presence of some substance or substances actually detrimental to plant development and not to the absence of beneficial nutritive substances.

In Plate I, figure 2, is shown another experiment, in which both carbon black and ferric hydrate were used as absorbents for the toxic substances. Both treatments show a marked development in plant growth over the original soil extract. This property is possessed by many other finely divided solids, as has been pointed out in previous bulletins.

Merely diluting the extract of a poor soil with distilled water often improves it. This is well shown by the plants illustrated in Plate II, figure 1. The experiment there depicted was performed by Mr. F. R. Pember, at Ames, Iowa, while engaged in cooperative work with the Iowa experiment station. An aqueous extract of Iowa loess soil which had been reduced in productive capacity by continuous corn culture was diluted with various amounts of distilled water and wheat seedlings grown in the series of dilutions.

It will be noted from the illustration that the plants which grew in the original soil extract were inferior in root development to those which grew in distilled water. The roots produced in the

poor soil extract were not only short, but were thickened and discolored at the tips. With increasing dilution this root development was improved, the coarse, stubby roots being changed to long, fine roots. As shown in No. 6, the root development resembles, though it does not equal, that in the manure extract shown in No. 7. Evidently this soil extract contained some substances which had a toxic effect upon the plants in the original solution. When that solution was diluted with distilled water, the toxic substances were so decreased that the plants were able to make a better growth in spite of the decrease in amount of nutrients. To attribute this increase in development to a mere dilution of the mineral plant food constituents is hardly possible, in view of the fact that the treatment with absorbing solids like carbon black, ferric hydrate, etc., in which there was no dilution or diminution of these mineral constituents, produced even more marked effect on the root development, as did also the mere addition of a minute amount of a soluble organic substance, pyrogallol, as will be shown later. Moreover, the addition of manure extract, as shown in No. 7 in the figure, in which both mineral plant-food constituents and organic matter were added, had this same effect, whereas the addition of chemical fertilizers, while they increased the growth of tops, had no such marked effect on the root system of wheat seedlings grown in this soil extract. The marked effect of the organic matter of the manure extract in producing a healthy root development, when added to toxic soil extracts, has already been shown in Bulletin 36.

In further illustration of the effect of dilution of a poor soil extract, the results obtained by Mr. J. F. Breazeale at Ithaca, N. Y., while engaged in cooperative work with the Cornell experiment station, may be cited. Putting the total growth in the soil extract prepared from a sample of Dunkirk clay loam from a field of low agricultural value at 100, the growth when diluted with an equal volume of distilled water was 113.

Marked improvement may be obtained in the case of certain soils or soil extracts by the addition of organic compounds which can not be considered as plant nutrients in any sense. There has previously been described an experiment [a] in which the growth of wheat plants was increased 101 per cent by the addition of pyrogallol to the soil, the plants being grown in the soil itself. In another experiment [b] the growth of wheat in the extract of the soil was increased 38.6 per cent by the addition to the extract of 10 parts per million of pyrogallol. In some soil extracts even much smaller amounts produce quite remarkable effects, especially in root development, resembling in this respect the action of the manure extract. Recently similar

[a] Bul. 28, Bureau of Soils, U. S. Dept. Agr., p. 18. [b] Ibid., p. 22.

effects have been obtained by the use of 5 to 10 parts per million of alpha naphthylamine.

In Plate II, figure 2, are shown some results obtained with the extract of another Iowa soil, the Kansan till. Nos. 4 and 5 are duplicates of soil extracts, and 6 is a distillate from the extract. Nos. 7, 8, and 9 are the soil extract treated, respectively, with carbon black, ferric hydrate, and calcium carbonate, the solids being removed again by filtration, and illustrate well what has already been said about the absorbing properties of these bodies, although it is also possible that the carbonate produced a more deep-seated change. The usual coarse roots are changed to a finely branched and much elongated system. No. 10 shows strikingly the effect of adding 2 parts of pyrogallol to a million parts of the original soil extract which produced the plants with stunted roots shown in Nos. 4 and 5.

A further illustration of this action is that observed with the extract of the Dunkirk clay loam at Ithaca, N. Y., where 2 parts per million of pyrogallol gave an increase in total plant development of 34 per cent over that in the original soil extract, 4 parts per million gave an increase of 43 per cent, and 8 parts per million an increase of 70 per cent. In the extract from another unproductive soil from Takoma, Md., 8 parts per million of pyrogallol produced an increase of 37 per cent, while the same quantity of alpha naphthylamine produced an increase of 25 per cent in total plant development.

These organic substances can not be considered as plant foods and are, moreover, added in such small amounts that the increased growth could not be attributed to direct nutrition. Their action must, therefore, be ascribed to a different one from that of nutrition and that of the absorbing solids. Their action may be on the plant itself, causing it to resist the toxic effect of the soil solution, or else these substances, being chemically quite active, have themselves acted on the toxic substances in solution, causing them to become innocuous in their effect on the roots, perhaps by rendering them insoluble or producing more deep-seated chemical changes.

In some poor soil extracts the toxic property can be removed by distillation, and may then be found in the distillate. Thus in an experiment performed by Mr. J. F. Breazeale, while engaged in cooperative work with the Cornell experiment station, the distillate from the poor Dunkirk clay loam was more toxic to wheat seedlings than the original extract, and the boiled extract was much improved. Expressing the growth of wheat seedlings as measured by green weight of tops as 100, the distillate was 81, the boiled extract was 143. Pure distilled water cultures grown at the same time gave as good a growth of top as the extract—namely, 100—but the roots in the distilled water were much superior to those in the extract, and were practically identical in development with those in the boiled extract.

FIG. 1.—SHOWING THE TOXIC PROPERTY OF THE EXTRACT FROM AN UNPRODUCTIVE SOIL.

[Wheat seedlings grown in: 1, Pure distilled water; 2, toxic soil extract; 3, same soil extract from which the toxic substances have been removed by absorption with carbon black.]

FIG. 2.—SHOWING THE EFFECT OF ABSORBING AGENTS IN REMOVING TOXIC SUBSTANCES FROM SOIL EXTRACTS.

[Wheat seedlings grown in: 1, Poor soil extract; 2, same soil extract after removing the toxic substances by absorption with ferric hydrate; 3, same soil extract after removing the toxic substances by absorption with carbon black.]

In this connection attention should again be called to the fact that ordinary distilled water is frequently toxic to seedlings, algæ, etc., and is then quite unfit for such physiological investigations. For the literature on this subject and a detailed investigation of these properties, the reader is referred to the work of Livingston in Bulletin 36 of this Bureau.

Ordinary distilled water obtained by distillation of well or even river water is virtually a distillate of a soil extract, and it is therefore not surprising to find a similarity between the two distillates in respect to this toxicity. By distillation it is possible even to increase the toxic effect in the first portions which come over. It may also be noted here that rain water is better suited physiologically for such experiments than is ordinary distilled water obtained from certain sources. This is erroneously attributed by some to the ammonia, nitrite, and nitrate contained in the rain water, although the amount present is entirely inadequate for producing an increase in plant development in such experiments. It is much more probable that the continued exposure of water in the vapor form to the air under the influence of sunlight brings about an oxidation of such toxic substances, which, when the distillation is done in the laboratory, escape this continued action of the air, and the vapors are, moreover, seldom, if ever, exposed to the sunlight, so that it is necessary to resort to more violent oxidizing agents like chromic acid, permanganate, etc., in order to obtain physiologically pure water by mere distillation in the ordinary laboratory stills.

Mere boiling of a poor soil extract for a short time has in some cases produced quite striking results, and such an experiment is shown with flax seedlings in Plate III, figure 1. As is seen from the photographs, the flax seedlings in the untreated extract are very poorly developed. The roots scarcely developed at all, and were very coarse and stubby as well as much discolored. The addition of plant nutrients in abundant amounts was capable of forcing the tops, but the impoverished root system remained as shown in No. 4. Treatment with carbon black in the manner already described gave the fine plants with well-developed roots, shown in No. 3, and obviously added no nutrients, but on the contrary removed from the extract something actually deleterious to flax development. Still more striking, and this is the particular point to be emphasized here, is the result obtained by merely boiling this extract for one minute. The fine growth of plants obtained is shown in No. 2, and the conclusion that very volatile or thermolabile substances deleterious to flax were present in the extract can not be avoided. The green weights of the plants, taking the untreated extract as 100, was 176 for the boiled extract, 197 for the carbon-treated extract, and only 138 for the addition of fertilizer salts. Nos. 1, 2, and 3 obviously contained

practically the same amount of mineral nutritive substances, yet the growth is quite different in the last two, whereas No. 4 contained a much increased amount of plant nutrients without producing as good an effect as the two simple treatments. The effect of the fertilizer salts appear, in fact, to have been in this case a stimulation of growth rather than an amelioration of the toxic conditions.

The extract from a poor soil may often be benefited by incineration or mere charring of the organic matter present in the residue obtained by evaporation and redissolving in pure water.[a] When plants are grown in such a solution they show marked improvement over those grown in the original extract. In the experiment cited, 24 wheat plants grown in the solution showed an increase of 25 per cent after incineration over a control in the original extract. Here there has apparently been a destruction of the substances which were previously detrimental to the growth of the plants.

This and other facts indicate that the toxic substances are organic in their nature. In more extended studies there was much evidence that at least part of the toxic conditions of the soil were transmitted to it by growing plants. The experimental facts which confirm this assumption are given in the following pages.

THE DIMINISHED YIELDS OF SUCCEEDING CROPS.

When one crop is continually grown upon the soil the yields usually show a decline. In course of time the land may become unfit for the growth of that plant, but another plant will thrive where the former failed. Since the causes of the decreased yield affect the whole period of the plant's growth, instructive data are furnished by the growth of young plants in pots.

Table I shows the records of the growth of wheat plants in paraffine wire pots.[b] In each case the green weight of the first crop is expressed as 100, and the weights of the succeeding crops are expressed in figures which show the relation to the first crop. In some cases a third and fourth crop were obtained, and they show a continually decreasing yield.

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[a] Bul. 28, Bureau of Soils, U. S. Dept. Agr., p. 29, et. seq.

[b] This method of pot culture has been fully described in Circular 18 of this Bureau and in Farmers' Bulletin No. 257, U. S. Dept. Agr.

TABLE I.—*Showing the effect of continuous planting to wheat in the paraffined wire pots.*

Number.	Soil type.	Relative green weight of tops.			
		First planting.	Second planting.	Third planting.	Fourth planting.
1	Cecil clay	100	68	57	44
2	Leonardtown loam	100	30	37	23
3	Takoma lawn	100	53	53	46
4	Cecil clay	100	(a)	61	40
5	Leonardtown loam	100	(a)	32	32
6	Portsmouth sandy loam	100	64	30	.....
7	Hagerstown loam	100	60	41	.....
8	Norfolk sandy loam	100	78	.....	.....
9	Cecil sandy loam	100	105	.....	.....
10	Arlington clay loam	100	51	.....	.....
11	Miami loam	100	55	.....	.....
12	Miami clay loam[b]	100	58	42	.....
13	Miami silt loam	100	72	.....	.....
14	Portsmouth sandy loam	100	35	.....	.....
15	Cecil silt loam	100	65	.....	.....

[a] No new control for comparison. [b] By transpiration.

Many, perhaps a majority, of agricultural students would infer from such results that the soil had been depleted of plant nutrients by the first crop. There is now evidence from a number of sources that the diminished yield is due to the presence of substances deleterious to plant growth. The addition of plant nutrients at the time of planting the second crop often fails to produce a yield equal to the first. Tables II, III, and IV show the results of experiments on several different soils in which fertilizers ordinarily regarded as supplying plant foods were added to these soils at the time of planting.

TABLE II.—*Results for the first and second crops when the same fertilizers were applied prior to planting each crop.*

Number.	Treatment.	Green weight of wheat.	
		First crop.	Second crop.
1	Untreated control; first crop in each case	100	100
2	Replanted without fertilizers	.....	35
3	100 parts per million of $NaNO_3$, K_2SO_4, and $CaH_4(PO_4)_2$	130	46
4	100 parts per million of $NaNO_3$, K_2SO_4, and $CaH_4(PO_4)_2$ + 1,000 parts per million lime	205	115
5	2,500 parts per million cowpeas	157	73
6	2,500 parts per million cowpeas + 500 parts per million lime	200	91
7	5,000 parts per million cowpeas	204	90
8	5,000 parts per million cowpeas + 1,000 parts per million lime	238	112

TABLE III.—*Results for the first, second, and third crops when the fertilizer treatment on the first crop was repeated on the second but omitted on the third crop.*

Number.	Treatment.	Green weight of wheat.		
		First crop.	Second crop.	Third crop.
1	Untreated control; first crop in each case	100	100	100
2	Replanted without fertilizer	.....	64	30
3	200 parts per million of $NaNO_3$	127	91	40
4	100 parts per million each of $NaNO_3$, K_2SO_4, and $CaH_4(PO_4)_2$	123	86	25

TABLE IV.—*Results for the first, second, and third crops. The fertilizer treatment was omitted on the second crop but applied to the third crop.*

Number.	Treatment.	Green weight of wheat.		
		First crop.	Second crop.	Third crop.
1	Untreated control; first crop in each case	100	100	100
2	Replanted without fertilizer		60	41
3	Stable manure 10,000 parts per million	87	58	45
4	1,000 parts per million lime	100	65	56
5	100 parts per million each of $NaNO_3$, K_2SO_4, and $CaH_4(PO_4)_2$	119	59	62
6	2,500 parts per million cowpeas and 500 parts per million lime	100	74	77

In these tables the green weight of the plants grown on untreated soil is taken as 100 and the weight of all other crops expressed in terms of that control. A fresh control was always planted for comparison with a replanted series.

It will be noted that in most cases the yield was not maintained equal to that of the first crop on untreated soil. In those cases in which the yield of the second or third crop was maintained it will be noted that it was due to the application of materials which are not primarily valuable on account of the plant food constituents which they contain. Lime and green manures were more efficient in maintaining the yield than such plant-food constituents as nitrogen, potash and phosphorus. The yield of the second and third crops was never maintained by the mineral fertilizers, while it often was kept up by the lime and organic manures.

It would seem, therefore, that the purely mineral fertilizers are not as efficient, if indeed they exert any action at all, as the organic manure or lime in overcoming the bad conditions arising as the direct and immediate result of the growth of the seedling plants. When the organic excretions are however allowed to change by the action of air or microorganisms, it might be possible that even these types of mineral fertilizers would be effective, either directly or indirectly, in overcoming the bad effects of the changed excretions.

TABLE V.—*Relative results for the first and second crops when the soil was given a new treatment by different fertilizer for the second crop—Cecil silt loam.*

Number.	First crop.		Second crop.	
	Treatment.	Green weight.	Treatment.	Green weight.
1	Untreated control	100	Untreated control (first crop)	100
2			Replanted without any fertilizer	65
3	10,000 parts per million stable manure.	110	100 parts per million $NaNO_3$	66
4	100 parts per million $NaNO_3$	174	100 parts per million each of $NaNO_3$, K_2SO_4, and $CaH_4(PO_4)_2$.	83
5	100 parts per million each of $NaNO_3$, K_2SO_4, and $CaH_4(PO_4)_2$.	167	1,000 parts per million lime	63
6	5,000 parts per million cowpeas	236	1,000 parts per million lime	74
7	2,500 parts per million cowpeas and 500 parts per million lime.	200	2,500 parts per million cowpeas and 500 parts per million lime.	111

In Table V there are reported the results of an experiment in which the fertilizer treatment was varied for the second crop. If the question of these second-crop yields be considered one of improper ratio of plant nutrients, it might be expected that a variation in fertilizers might be of benefit. There is no evidence, however, that the second-crop yield received any increased benefits from such a treatment. The only treatment which maintained the yield was an application of green manure and lime, as in the previous experiments.

These results can only be regarded as strong evidence that the diminished yields of a second crop in these experiments are not due to the removal of plant nutrients by the first crop. In the first place, the growth of wheat plants for three or four weeks could not possibly exhaust the soil of soluble minerals. Moreover, the addition of a complete mineral fertilizer in an amount greater than the first crop withdrew is unable to maintain the original yield. Surely no one would argue that the application of green manure and lime add more mineral plant nutrients than were given, for example, in treatment No. 4, Table V, for the second crop. While the results obtained are the strongest kind of evidence that the benefit of the fertilizers was not in adding nutrients, they also show that certain fertilizers may act beneficially upon the soil or upon something which it contains. Since the first crop was decidedly better than the second crop, the natural conclusion is that the decrease is a result of conditions imposed by the growth of the first crop.

Further proof on this point was obtained in an experiment which demonstrated that toxic substances were given off by the seedlings during germination. Five pots of soil were planted with wheat which had just begun to germinate. The wheat was allowed to grow only five days, a length of time obviously insufficient to exhaust the soil of plant food. By that time roots had been developed, and the tops had just appeared above the surface of the soil. All the plants were carefully removed from the pots of soil and a new crop planted. At the same time five similar pots of soil which had not been planted to anything were planted to wheat to serve as controls. The wheat was allowed to grow sixteen days under optimum conditions. The crop which grew in the soil where the previous crop of wheat had germinated was decidedly inferior to that in the soil which had supported no growth of wheat. The growth of the crops was measured both by the amount of water transpired and by the green weight of the tops. The transpiration of the crop which followed the germinating wheat was 63 per cent of the transpiration of the control, and their green weight was 81 per cent of that of the control series.

That infertility is not due to lack of plant nutrients is also shown by the fact that highly enriched market gardens often become unpro-

ductive. Recently the Minister of Agriculture of France[a] has described the failure of crops in the old and highly enriched gardens of that country. Since the failure of crops has never been shown to be due to bacterial or fungous diseases of the plants, they assume that the cause of the difficulty is in the soil. The analysis of such soils shows that they are abundantly supplied with plant nutrients, yet there is a notable failure in the attempt to grow crops which at one time flourished on these soils.

Further experiments have been conducted, which afford strong evidence that the poor growth of the second crop is not a question of plant nutrients. The same experiments agree in indicating that the first crop leaves behind substances which are toxic to the second crop.

A typical experiment may be quoted from Bulletin 28 of this Bureau (p. 34). Wheat was planted in a series of five pot cultures of clean glass sand simultaneously with five other pot cultures planted in glass sand, which had previously grown wheat for twenty-one days. The two series were subjected to the same conditions of growth measured by the amount of water which the plants transpired. The growth of the plants in the "exhausted" sand was about 45 per cent of that in the fresh sand. In the same experiment the effect of a good absorbing agent was tried. Ferric hydrate was added to five pots of "exhausted" sand in which wheat was planted. This good absorbing agent renovated the sand to such an extent that the growth of wheat in it was only 6 per cent less than that in the fresh sand.

It would not be correct to assume that the decreased growth in the sand was due to the depletion of nutrients. Neither can one maintain that the beneficial action of ferric hydrate consisted in supplying nutrients. The only plausible explanation is that the ferric hydrate had a strong absorbent action upon some substance, or substances, which were toxic to the second crop of wheat and which had resulted from the growth of the first crop.

Another experiment was performed to demonstrate more clearly the way in which the deleterious products of plant growth affect succeeding crops of the same species. Three crops of wheat seedlings were grown in paraffined wire pots, using a soil of low productivity. The third crop produced a green weight of 4.73 grams, in contrast to 9.9 grams, the weight of a first crop grown at the same time in fresh soil. An aqueous extract was prepared of the soil which had produced three crops of wheat and used as a nutrient solution for plants. Plate III, figure 2, shows the plants which grew in this extract of an "exhausted" soil before and after treatment with

[a] Bul. Mensuel de l'office de Renseignements Agricoles, 4, 1079–1082, 1905.

carbon black. No. 1 shows the plants growing in the untreated extract from the "exhausted" soil; No. 2, the plants which grew at the same time in an extract of fresh soil which had not grown wheat. The plants shown in No. 1 weighed 2.40 grams. Those in No. 2 weighed 3.04 grams. Another portion of each of the aqueous extracts was treated with an absorbing agent, in this case carbon black. No. 3 represents the plants which grew in the treated extract of the "exhausted" soil, and No. 4 the plants grown in the treated extract of fresh soil. The fresh weight of the plants in No. 3 was 4.15 grams; of those in No. 4 was 4.07 grams.

The growth of the plants in the extract of an "exhausted" soil after treatment with carbon black is emphatic evidence that there was still a sufficient supply of plant nutrients in the soil. When both extracts were treated similarly they gave plants having so nearly the same weight that the difference is entirely within the range of individual variations. The experiment proves that the decrease of growth was due to the formation of some toxic substance in the soil of the pots during the growth of the preceding crops. The absorbing agent removed this deleterious material, and then the growth was as good as that in the fresh-soil extract similarly treated, and superior to the growth obtained in the untreated extract from the fresh soil, which, as mentioned above, was itself a soil of low productivity and capable of improvement by this method of treatment.

Many well-known facts point to the same conclusion as that drawn from these laboratory experiments. A repetition of the same crop on ordinary land is not generally profitable, but a different crop will thrive, although it requires the same elements as food and in nearly the same amounts. It is a matter of common knowledge that an orchard tree planted in the place of one which died after making a few seasons' growth rarely succeeds. The replanted tree usually makes an unsatisfactory growth and often dies, even when fertilizers are added. In greenhouse practice it is found better to transplant seedlings several times than to attempt to grow them in one soil continuously. No one would presume to assert that young seedlings which are partly nourished by the reserve materials of the seed can, in a few weeks, exhaust the soil of plant nutrients. If, on the other hand, the soil is rendered insanitary by the growth of the roots or by excretions from them, the beneficial effects which naturally follow transplanting are intelligible.

MUTUAL EFFECTS OF THE ROOTS OF TREES AND OTHER PLANTS.

There is not only a deleterious effect of a given plant upon its own kind, but, in certain cases, upon different plants. Such successions are to be avoided in crop rotations as much as the continuous growth

of a single crop. It is known that certain crops do not thrive when planted on newly cleared land which was originally covered with walnut or butternut trees. It has been observed that rye grass, certain Erigerons, and the tares seem to "poison" wheat. Thistles are said to "poison" oats and Euphorbias to kill flax.

The antagonistic effect of one plant upon another is perhaps no better brought out than in a study of the effects of grass upon apple trees at the Woburn Experimental Fruit Farm.[a]

The authors of that report found that young apple trees were severely injured when grass was allowed to grow about them. In 1897 they began to notice the harmful effect produced by grass upon their fruit trees, especially apple and pear trees. Their first supposition was that it was due to the removal of plant food, and so they inaugurated experiments to determine if this assumption were correct, but all their experiments answered the question in the negative. They then investigated to see whether the removal of water by the grass was the cause, but here again they received only a negative answer. During the successive years up to 1904 they tried the effect of carbon dioxide on the trees, thinking that this might be given off by the grass in such large quantities as to be harmful. This proving not to be the cause, they tried the effect of the exclusion of oxygen and of packing due to the sod formed by the grass, but in all cases they were baffled, finding no evident effect of any of these factors on the trees. The successive reports show most interesting work and elaborately carried out experiments.

Having ruled out all the above-mentioned factors, they found by other experiments that only the most actively growing portions of the tree root system was affected by the grass. A circular sod of a few feet in diameter around the tree had no effect, but as the circle was increased the tree began showing the effect of the grass, viz, a stunting of the tree, a premature falling of the leaves, with entire change of the normal color of the fruit from green to red. In very many instances the trees were killed outright. They also found that the pernicious effect of the grass was strongly marked even when only one one-thousandth to one two-thousandth of the root system of the tree was exposed to the action of the grass.

Finally, after about seven years of work, they concluded that the pernicious effect of the grass could be due only to some action on the tree akin to that of direct poisoning, leaving the question open as to whether this action is due to direct excretions from the grass or to a changed bacterial action in the soil induced by the presence of the grass. They state their belief that the grass has some actively malignant effect on the trees akin to direct poisoning.

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[a] Rept. Woburn Expt. Fruit Farm, 1900, 1903, 1904.

FIG. 1.—SHOWING THE EFFECT OF DILUTION OF A SOIL EXTRACT HAVING TOXIC PROPERTIES.

[Wheat seedlings grown in: 1, Distilled water; 2, extract of poor loess soil; 3, four parts soil extract and one part distilled water; 4, three parts soil extract and two parts distilled water; 5, two parts soil extract and three parts distilled water; 6, one part soil extract and four parts distilled water; 7, forty parts soil extract and one part manure extract.]

FIG. 2.—SHOWING THE EFFECT OF PYROGALLOL AND OTHER TREATMENTS ON A SOIL EXTRACT HAVING TOXIC PROPERTIES.

[Wheat seedlings grown in: 4 and 5, Soil extract untreated; 6, distillate from the soil extract; 7, soil extract treated with carbon black; 8, soil extract treated with ferric hydrate; 9, soil extract treated with calcium carbonate; 10, soil extract treated with pyrogallol (2 parts per million).]

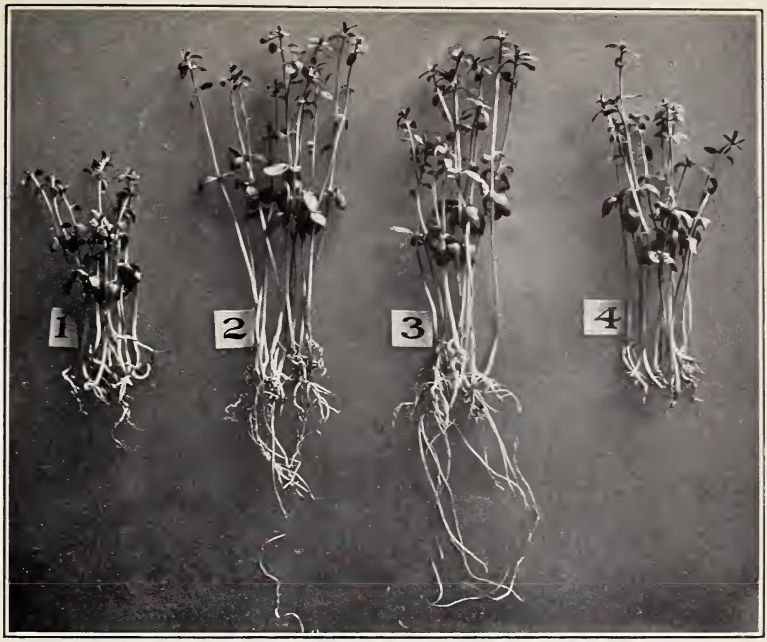

FIG. 1.—SHOWING EFFECT OF BOILING AND OTHER TREATMENTS ON A SOIL EXTRACT HAVING TOXIC PROPERTIES.

[Flax seedlings grown in: 1, Soil extract untreated; 2, soil extract boiled 1 minute; 3, soil extract treated with carbon black; 4, soil extract plus salts of a complete plant nutrient solution (112 parts per million).]

FIG. 2.—SHOWING EFFECT OF SUCCEEDING CROPS IN THE SOIL AND THE EFFECT OF CARBON BLACK IN IMPROVING THE EXTRACT FROM THE "EXHAUSTED" SOIL.

[Wheat seedlings grown in: 1, Extract of a soil which had produced three crops of wheat in pots; 2, extract of fresh soil; 3, portion of same extract used for No. 1, treated with carbon black; 4, portion of same extract used for No. 2, treated with carbon black.]

Jones and Morse[a] report a similar antagonism to exist between butternut trees and the shrubby cinquefoil. The cinquefoil was often killed under and around the butternut trees on a circle fully twice the diameter of the tree top. Upon examination they found that in every case the roots of the dead or dying cinquefoil were in close proximity to those of the butternut trees. They say further:

> Moreover, with such butternuts the "dead line" for the weed is pushed outward year by year as the tree enlarges, so that the trees may be surrounded by a circle of dead and dying cinquefoil plants bordering the clean grassy plot under the tree. This antagonism is, we believe, attributable rather to the root relations of the two plants than to those of shade. Thus young butternuts from 2 to 8 feet high were observed to be surrounded by a circle which might be twice the diameter of the top of the tree, within which the weeds were dead and with dying plants bordering its margins. Such butternuts do not cast much shade. Moreover, young birch, beech, maple, cherry, apple, and pine trees in the same field showed no such striking relation to the death of the cinquefoil, healthy plants of the weed frequently crowding close under their branches.

An interesting observation which showed that the antagonistic influence of the butternut trees is from the roots, rather than from the foliage, is given:

> Near a large mature butternut tree and well within the circle where the weeds had elsewhere been killed, several green, healthy cinquefoil plants were observed in striking contrast to the rest of the circle. Upon investigation it was found that these were growing in very thin soil, overlying a ledge which so rose as to form a barrier over which no butternut roots had passed in this direction.

No evidence of root parasitism was detected in any case.

More recently an antagonism between peach trees and several herbaceous plants, commonly used as cover crops in orchards, has been reported by Hedrick.[b] That investigator found that young peach trees planted in large pots, in which oats was also planted, shed their leaves and matured early. The foliage of these trees was never as abundant as of the others, and before falling, it turned yellow. The trees grown in pots in association with potatoes and tomatoes were found to be next in order of injury, but the yellow color of the foliage was not as marked with the potatoes and tomatoes as with the grains. Trees grown with mustard or rape were also slightly checked in growth, whereas those grown with beans and crimson clover were not thus affected.

In the course of some experiments conducted by this Bureau on a lawn in Takoma Park, Md., it was found almost impossible to maintain a growth of grass or clover in the vicinity of oak, pine, and other trees. Stable manure was thoroughly incorporated with the

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[a] Ann. Rept. Vermont Agr. Expt. Sta., **16**, 173–190, 1903.

[b] Proc. Soc. Hort. Sci. 1905, pp. 72–82.

soil, and later artificial fertilizers were added. The grass and clover grew well for a time, but were soon checked and finally died in spite of good care.

When the plats had been originally spaded up, many tree roots were encountered and removed. After the death of the grass, when the plats were again spaded up, they were found to be almost completely filled with young, actively growing tree roots, the special preparation of the soil having been very favorable for the growth of the tree roots.

As the lawn, which is very unfavorable for the growth of grass, is everywhere permeated with tree roots, it was thought that they might exercise some malignant effect upon the growth of grass. Accordingly, experiments were performed to obtain evidence upon this question. In order to control the different factors influencing growth, experiments were conducted in a greenhouse by Mr. C. A. Jensen with small trees in paraffined wire pots. A number of tree seedlings, varying in height from 15 cm. to 40 cm., were dug up and planted in paraffined wire pots. The species of trees gathered were pine, tulip, maple, dogwood, and cherry.

Two pots of soil were put up without trees for comparison, and these received the same treatment during the experiment as the pots containing the trees. The same number of germinated wheat seeds was planted in each pot and all watered from time to time as necessity demanded. The first crop of wheat was removed on June 29 and another lot of germinated wheat seeds planted. Each crop grew from two to three weeks, and the experiment was continued till December 8.

Two pine seedlings were planted at first, but during the growth of the first crop of wheat one of these died, but the paraffined pot was left in the experiment and continued to receive the same treatment as the others.

The following table shows the results of each crop, the green weight of the wheat plants being used as the criterion of growth:

TABLE VI.—*Relative green weights of wheat crops grown in association with tree seedlings.*

Date of harvesting.	June 29.	July 12.	Aug. 1.	Aug. 22.	Sept. 6.	Oct. 13.	Oct. 29.	Nov. 19.	Dec. 8.	Average of first 6 crops (summer).	Average of last 3 crops (autumn).
Control	100	100	100	100	100	100	100	100	100	100	100
Maple 1	76	65	86	68	67	86	92	91	96	74	93
Maple 2	44	86	75	59	71	89	90	75	109	71 72	91 92
Maple 3	21	83	72	72	79	84	81	103	92	70	92
Dogwood 1	92	96	76	84	71	65	83	68	115	81 79	89 91
Dogwood 2	86	79	63	86	75	73	84	107	88	78	93
Cherry	81	91	102	91	71	94	88	102	93	88	94
Tulip	21	106	82	77	68	100	77	109	103	76	96
Pine	55	69	68	52	54	80	62	83	60	63	68
Pine (dead)	62	96	85	91	80	89	97	96	67	84	87

Representing thus the weights of the plants in the control pot as 100, those with the cherry gave 88, dogwood 79, tulip 76, maple 72, living pine 63, dead pine 84, these figures being the average of the six summer crops with each tree species up to October 13. It seems, therefore, that the presence of the tree roots had a harmful effect on the growth of the wheat. That the harmful effect was due to substances excreted by the tree roots seems probable, for the small size of the pots used made it necessary for the two kinds of roots to be in close physical relation. There are several facts which lead to this conclusion. An inspection of the table shows an evident increase in yield of wheat tops when the physiological activities of the trees were diminished by their entering upon their seasonal rest in autumn. It was also noticed that the tree pots that produced as much wheat growth in November, as the controls were those in which the trees showed the earliest signs of winter rest. Attention should be called to the fact that if the trees had removed sufficient plant food to starve the wheat plants in the summer period the increase in yields toward autumn would be incapable of explanation.

The increase in wheat growth in the various pots toward autumn is more clearly brought out in the last two columns of the table. The first shows the average yield of six crops, which grew between June 15 and October 13, a period in which the physiological activity of the trees was the greatest. The second of these columns shows the average of the three following crops. It will be seen that there is a decided increase in the average yield of the last three crops, except in the case of the dogwood, and it was the last deciduous tree to shed its leaves, having only lost them just before the last crop of wheat was removed on December 8.

The two pine seedlings present an interesting case. The pot containing the dead tree produced a greater yield of wheat than that containing the living tree. At the same time it should be noted that the pot containing the dead pine never equaled the control pots in producing a yield of wheat, although there was no more plant food being removed than in the control pots.

It should be mentioned that in replanting the wheat the roots of the previous crop were left in the soil. The organic matter of the wheat roots would thus act as a light application of green manure, although it is well known that wheat is not very effective as green manure. This would, perhaps, even help slightly to counteract the deleterious effect of the tree roots on the wheat.

Summarizing the foregoing, we find that seedling trees of tulip, dogwood, maple, cherry, and pine retard the growth of wheat when the latter is grown under conditions requiring its roots to be in close physical relations with the tree roots. The retarding effect differs

with different species of tree seedlings, the greatest retardation occurring during the season when the tree seedlings are in the most active physiological condition. The harmful effect becomes less as the trees enter upon their period of winter rest.

This injurious effect of tree seedlings upon wheat appears to be due to the excretion of substances by the tree roots which are toxic to wheat.

That excretions from other parts of the plants than roots are poisonous has also been shown. The washings from the bark of trees and from leaves have been shown to be decidedly toxic to wheat plants[a] and to grass. The retention of these washings by the soil is undoubtedly a factor in the infertility of the soil in the vicinity of such trees. It is well known that terpenes, such as turpentine, and terpene derivatives, like the camphors, which may be regarded as excretions of certain trees, have a deleterious effect upon plants.[b] Heller[c] has made the interesting observation that the plants which secrete terpenes are less susceptible to injury by them than are plants in which terpenes do not occur.

THE EFFECT OF PLANTS ON THE MEDIUM IN WHICH THEY GROW.

Some evidences of the formation of toxic conditions during plant growth have already been given in former bulletins. An experiment which is described in Bulletin 28, page 35, indicates quite clearly that toxic substances arise during growth. It consisted in placing an absorbing agent in a synthetic nutrient solution and measuring the growth of wheat plants in it. The plants from the nutrient solutions containing carbon black grew 27 per cent more than the control plants in a solution in which carbon black was lacking. In the solutions containing ferric hydrate the growth was increased 33 per cent. In another experiment, water redistilled from potassium dichromate and sulphuric acid and from alkaline potassium permanganate was used, the distillates being condensed in a platinum tube. The addition of ferric hydrate to part of the cultures produced an increase of growth (measured by transpiration) amounting to 34 per cent. The conclusion was there drawn that the roots of seedling wheat plants do give off substances which are poisonous to themselves, and that these substances can be removed or corrected by carbon black or ferric hydrate.

Since it has been shown in this and in the earlier bulletins from this Bureau[d] that many soils owe their unproductiveness to the

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[a] Bul. 36, Bureau of Soils, U. S. Dept. of Agr., 1906.

[b] Riedlin. Dissertation München, 1887; Effront. Comp. rend 136, 1556, 1903; Chamberland. Ann. Inst. Pasteur, 1887, p. 153.

[c] Heller, Flora, **93**, 1, 1904.

[d] Bul. 28, Bureau of Soils, U. S. Dept. Agr., 1905; Bul. 36, Bureau of Soils, U. S. Dept. Agr., 1906; Breazeale, Bot. Gaz., **41**, 61, 1906.

presence of toxic substances and that toxic conditions are brought about by the growth of even a single crop of wheat seedlings, as shown in the foregoing pages, the question comes up whether some of these toxic substances may not be excretions from the roots of growing plants. The works cited above give some indications that such substances are formed by growing plants. The supposition is rendered more probable by the experiments related in Bulletin 36 of this Bureau, which point rather strongly toward the organic nature of the toxic substances. Also by the data given below, which show that the excretion of toxic substances is known in certain groups of the lower plants.

An examination of the literature, especially that dealing with the growth of the lower plants, shows that different workers have found that the growth of these plants often gives rise to unfavorable conditions in the surrounding medium.

Citations of a few laboratory experiments are given because they help to explain processes which occur in the soil.

Experimenters upon chemotropism have found that the growth of fungus hyphæ is not always in the direction of nutrient materials, but that they will sometimes grow into toxic substances. Clark [a] found that the hyphæ of Rhizopus would grow from a layer of rich nutrient agar into a layer of nonnutrient agar containing 0.005 N copper sulphate. Fulton [b] working on the same subject has clearly demonstrated that the hyphæ grow in any direction that will carry them out of a region already occupied by numbers of hyphæ. He showed that the repelling substance remains in the solution in which fungi have grown, and that it is not carbon dioxide. The results of the two last-named authors agree in indicating that the fungus hyphæ are negatively chemotropic to some substance which they excrete and this negative chemotropism is much greater than any positive chemotropism they may have for nutrients or oxygen.

According to Ferguson [c] the germination of certain mushroom spores is greatly facilitated when a small bit of living mushroom tissue is included in the culture, but the further development of hyphæ from these spores is almost completely inhibited. When the spores which have germinated are transferred to cultures in which there are no pieces of tissue a continued development of hyphæ takes place. This observation would seem to indicate that the pieces of living tissue exerted some influence which inhibited further growth and that its inhibitory effect was first felt by the delicate germ tubes.

Bacteriology has demonstrated quite distinctly that deleterious

[a] Bot. Gaz., **33**, 47, 1902.

[b] Bot. Gaz., **41**, 81, 1906.

[c] Bul. 16, Bureau of Plant Industry, U. S. Dept. Agr., 1902.

substances are formed during the growth of cultures. Eijkman[a] has studied the reaction of the waste products of a number of bacteria upon the same and other spores. He found that the organisms produced without exception thermolabile substances which inhibited growth. The inhibiting substances were diffusable, but could not be filtered through a porcelain filter; they were destroyed when heated to a temperature at which the organisms were killed. The waste products of a given species were usually more toxic to that and closely related species than to those species more distantly related.

Eijkman's results are confirmed by the recent work of Rahn[b] on other bacteria. Rahn finds a thermolabile toxic substance which is absorbed by freshly heated clay filters, so that a piece of recently heated clay saturated with old bouillon was quickly covered by a growth of organisms. The toxic substance was also destroyed by diffuse light.

The work of Emmerlich and Löw[c] and other investigators on the action of bacteriolytic ferments and toxic action of these on the bacteria of many infectious diseases involving the preparation of antitoxins and their use in medicine is of the greatest interest in this connection as showing that the products of bacterial life are poisonous to the living forms of a similar or related species.

The antagonistic action which is quite commonly seen among many of the lower plants is succinctly described by Pfeffer.[d] His summary is presented here on account of its inclusive survey:

> Fungi, bacteria, and many other of the lower organisms are able to conquer and kill their adversaries by means of certain poisonous excretory products, while by means of cellulose (dissolving) enzymes, parasitic fungi are able to penetrate a host plant. In reciprocal symbiosis, however, the exchanges are of mutual advantage.
>
> Even the normal excretory by-products may injuriously affect other organisms. Thus, 2 to 3 per cent of alcohol acts injuriously or fatally upon many organisms, although certain alcohol-producing species of Saccharomyces can withstand 14 per cent. Further, most bacteria and many other organisms are injured by even a slightly acid medium, and hence are suppressed and killed by fungi which produce large quantities of free acid without being themselves affected.[e] Thus, if yeast and bacteria are sown in an acid solution of sugar, the yeast attains the upper hand, whereas in an alkaline or neutral solution the bacteria rapidly develop and multiply, and the yeast is suppressed,[f]

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[a] Centralbl. f. Bakt., etc., I Abt., **37**, 436–449, 1904.

[b] Centralbl. f. Bakt., II Abt., **16**, p. 417, 1906.

[c] Zeitschr. f. Hyg., **31**, 1 (1889); Centralbl. f. Bakt., **31**, I, 1 (1902); Ibid., **32**, 821 (1902); Ibid., **33**, 627 (1903).

[d] Physiology of Plants (trans. by Ewart), Vol. I, p. 512.

[e] Wehmer: Beitr. z. Kennt. einheim. Pilze, 1893, p. 69; 1895, p. 143. Reinhardt: Jahr. wiss. Bot., **33**, 515, 1892: Wehmer: Bot. Zeit. 1891, p. 233; Ber. d. d. bot. Gesell., **24**, 381–384, 1906.

[f] Nageli. Die niederen Pilze. 1877, p. 31; Pasteur, Ann. Chem. Phys. 1858, III ser. T. 52, p. 415.

The antagonistic effect is not due to the fermentative activities of the yeast. The final result in all such cases depends upon the specific properties and reactive powers of the different organisms, as well as on the external conditions, i. e., upon several variable factors.

The higher plants do not seem to have been extensively studied in this regard, and an examination of the literature dealing with experiments on the growth of the higher plants fails, therefore, to reveal many indications of poisonous excretions. Newcombe,[a] in describing the growth of roots in closed glass tubes containing water, says that the roots suffered distortion after twelve to fifteen hours when the temperature was 23° C. or over. He referred the distortion to a possible lack of oxygen or to the accumulation of root excretions.

It is the purpose of the following experiments to show that the roots of certain higher plants may produce substances which have a deleterious effect, and that the undue accumulation of these substances in the soil is unfavorable for the growth of plants. All agricultural soils are continually exposed to the influences of roots, hence the study of root action becomes a factor in the study of soil fertility.

PLAN OF THE EXPERIMENTS.

Previous experiments on the toxic substances indicated that they are present in very small amounts and that refined methods must be used in their investigation. They are so small in amount that no chemical analysis of the soil has ever given any indication of them. The assumption on the part of Braconnot,[b] Walser,[c] Boussingault,[d] and others that these substances existed in sufficient amounts to be detected by chemical analysis kept other workers from investigating their nature and action.

By using the plant as an indicator it is possible, however, to detect the presence of the toxic substances. The following experiments were therefore so planned that the plant could be used as an indicator of the presence of deleterious substances in the substratum.

It is evident from what has been said that mere elongation of the root would hardly afford a satisfactory indication of small amounts of deleterious substances. The behavior of roots when stimulated by the presence of chemicals (chemotropism) is, however, sensitive enough to serve as an indicator, as has been shown by several workers.[e] It has been shown that the roots when so stimulated will curve

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[a] Bot. Gaz., **33**, 343, 1902.

[b] Ann. Chim. Phys., **72**, p. 32.

[c] Untersuch. über d. Wurzelausscheidungen. Dissert. Tübingen, 1838.

[d] Ann. Chim. Phys. **1**, p. 217.

[e] Miyoshi. Bot. Zeit. 1894, 1, and Flora, **83**, 76, 1894. Molisch. Sitzungsb. Wien. Akad., **102**, Abt. I, 423, 1893. Newcombe and Rhodes, Bot. Gaz., **37**, 23, 1904. Sammet. Jahrb. wiss. Bot., **41**, 611, 1905. Lilienfeld. Ber d.d. bot. Gesell., **23**, 91, 1905.

and grow toward nutrient substances and away from deleterious substances, if other sources of stimulation are eliminated. The best medium in which the plants are to grow for the purposes of experimentation is one which is as nearly nonnutrient as possible, because any inequality in the distribution of nutrients might influence the results.

The plants used were seedlings, which were supplied with nutrients from the seed.

The wheat seedlings used in these experiments were germinated in water by a method devised in the laboratories of this Bureau. It has proven so satisfactory for growing seedlings to use in water cultures that a description may be properly given here.[a]

The seedlings are germinated on a perforated paraffin plate which floats on the surface of a pan of water. This plate is made by dipping a piece of wire netting into melted paraffin. The meshes of the netting are 5 or 6 mm. wide and the dipping is continued with alternate cooling until the openings are decreased to a size allowing the needed contact with water but keeping the seeds from falling through. If the meshes get too small, or even completely filled with the paraffin, they can be opened with a hot wire or a small cork borer. This procedure gives virtually a thin, flat paraffin plate, which is made very strong by the wire gauze reenforcement. The paraffin plate is then floated just at the surface of a pan of water by means of several large corks pinned or wired to the under surface of the disks close to its circumference. By means of such an arrangement the plate is always at the surface of the water, although there may be a large loss of the water by evaporation from the pan.

A perforated cork plate has also been found to be very satisfactory and is more easily prepared than the one described above. Plates of sheet cork 6 mm. in thickness were thickly perforated with holes 3 or 4 mm. in diameter. The plates were dipped in melted paraffin long enough to saturate the cork, but they did not become thickly coated with paraffin. Such plates will sustain the weight of a layer of wheat seeds and float on the water of their own buoyancy.

The variety of wheat known as "Chul" has been found well suited for experimental work in soil extracts and nutrient solutions. After soaking the seeds in water for six to eight hours, they are spread in a thin layer on the floating paraffin plate. Under such conditions the germination progresses very evenly and gives a supply of seedlings which are practically uniform in size. The roots of the seedlings grow downward into the water beneath. If the water in the pan be changed daily there is rarely any harmful growth of molds on the seeds.

When required for use, the seedlings are very easily removed and

[a] See also Livingston. Plant World, 9, 13 (1906).

the roots are free from any adhering particles, as is always the case when germinated in sand, etc. The seedlings are already accustomed to an aqueous medium and proceed to grow immediately when put into culture solutions, whereas seedlings germinated in sand or moss require a certain time to become accommodated to their new environment. Another advantage is the ease with which a large number of seedlings may be obtained. A circular plate 25 cm. in diameter usually gives from 400 to 800 seedlings of uniform development.

In the first experiments clean quartz sand was used as a medium in which to grow the plants. Owing to the difficulty of filling tubes of small diameter and the necessity (described later) of rotating the cultures, the sand was not suited to the purpose of experimentation. After some preliminary tests agar-agar proved to be a very satisfactory medium to serve as a substratum. Agar-agar is a substance prepared from certain seaweeds. When boiled in water it melts and forms when cool a clear jelly resembling gelatine, but more consistent. The fibers of agar-agar were soaked in one or two changes of distilled water at room temperature to remove the slight amount of soluble matter present. The agar was then melted by boiling in distilled water in the ratio of 2 parts of agar to 100 of water. The melted agar was filtered through absorbent cotton and gave a preparation which remained clear when reheated. The agar was poured out and allowed to cool to a temperature between 35° and 38° C., at which temperature it was just beginning to harden. The previously sprouted seedlings were put in at this time and were firmly held when the agar became set. In agar prepared in this manner the root system developed in a perfectly normal manner. The roots were clean and white, and showed no distortion or swellings, as they do in unfavorable media. The behavior of the roots could be noted at any time through the transparent agar jelly. The glass receptacles in which the seedlings grew were always covered with black paper to exclude light. Since the agar jelly contained about 98 per cent of water, the plants were able to obtain an ample supply for growth. Small quantities of distilled water were added daily to keep the surface of the agar moist and to prevent the formation of fissures.

The remarkable freedom of the agar from growth of molds and bacteria showed how free it was from substances which might serve as nutrients. Although the jars containing the agar jelly stood open from four to ten days, they were very rarely infested with molds or bacteria, and the few plants that were thus infested were discarded from the results.

PRELIMINARY EXPERIMENTS WITH WHEAT SEEDLINGS.

The first experiments were designed to perfect a method of using the plant so that it would serve as an indicator of the deleterious root excretions, if such substances were produced.

The best results were obtained from the use of segmented glass tubes having small openings between the segments. The tubes were made from glass tubing having an internal diameter of 6 or 8 mm. Pieces of tubing 10 cm. long were closed at one end by fusion. Each of these pieces was then cut into three nearly equal lengths. These three segments were bound to a glass rod, leaving a space of 2 or 3 mm. between adjoining segments. They thus formed a straight segmented tube with narrow openings one-third of the distance from the top and bottom, respectively.

The segmented tubes were placed in a vertical position in small glass jars, the fused ends of the tubes resting on the bottom of the small jar. Pure nonnutrient agar, which had been washed in three changes of distilled water and melted in distilled water, as described in the preceding section, was poured into the jars until its level reached the tops of the cylinders. When the agar had cooled to a temperature between 35° and 38° C., the roots of a wheat seedling 3 days old were inserted in the open, upper end of each segmented tube.

The design of such an arrangement was to inclose the growing roots in a small space in which the toxic excretions would be confined. At the same time it provided, at intervals, small openings through which there would be some diffusion of the toxic products to the exterior. When the growing roots reached one of these regions from which diffusion was taking place, they would have a chance to respond to this unequal distribution of the deleterious substances. Such response would be plainly manifested by the growth of the roots toward regions where deleterious substances were less abundant. In other words, the roots might curve and grow out of the narrow openings between adjoining segments of the tubes.

The first experiment employed a total of 26 roots. The jars containing the tubes and seedlings were wrapped in black paper and stood in a well-lighted portion of the laboratory. At the expiration of six days it was found that 14 of the roots had turned from their normal downward course and grown out through the narrow openings into the surrounding agar. The experiment was repeated three times, using a total of 90 roots, 48 of which grew out of the tubes through the narrow openings. It will be noted that this is a response of 53 per cent of the roots employed.

Since these roots have a natural tendency to grow vertically downward (positively geotropic), there must be some stimulus acting at

the narrow openings which causes them to curve and grow out. The roots in these and later experiments showed no distortion nor signs of curvature due to injury (traumatropism). It seems justifiable, therefore, to conclude that the curvature of these roots was a response to the presence of some substances which were unfavorable to them. At the narrow openings the deleterious substances had partially diffused toward the exterior and the roots grew into regions of weaker concentration. This response brought the roots out into the agar surrounding the tubes. The same phenomenon of diffusion will explain why the roots did not find the agar in the lower part of the tubes as favorable for growth as that outside the tube.

The following experiment may be cited in further support of the above statements:

Several jars containing melted agar, which had cooled to a temperature between 35° and 38° C., were thickly planted with wheat seedlings. In a few days the roots of the seedlings completely permeated the masses of agar; they were allowed to grow for a week longer and then carefully pulled out, removing as little agar as possible. The agar was melted over a steam bath at a temperature of 70° to 80° C., filtered through absorbent cotton, and poured into clean jars. Controls were set up simultaneously which contained freshly prepared agar. Each lot of jars received a set of segmented glass tubes, and when the agar had cooled to the proper temperature wheat seedlings were inserted in the open ends of the segmented tubes. If the foregoing hypothesis regarding the presence and diffusion of toxic waste products be true, one would expect fewer roots to leave the segmented tubes when they were surrounded by a medium which already contained the waste products, because there would be a more equal concentration of them throughout the entire medium. This is precisely what was observed. Of 23 roots which grew in the used agar, only 8 curved and grew out of the tubes, a response of only 35 per cent. Of 13 control roots grown in fresh agar, 7, or 54 per cent, turned and grew out of the tubes. (This figure is confirmed by that obtained in the above experiment on a larger number of roots.)

There might be some doubt as to whether part of the response might arise from a deficient supply of oxygen in the small tubes, and the question "Do the roots in the tubes curve because of a possible insufficient supply of oxygen?" naturally presents itself. The evidence obtained by Bennett [a] is entirely against such behavior. The author just mentioned made very careful and exhaustive experiments with the roots of land plants, but was unable to find any evidence whatever that direction curvatures could be induced by the

[a] Bot. Gaz., 37, 241–259, 1904.

one-sided application of such gases as oxygen or carbon dioxide. It was deemed desirable, however, to test the roots of wheat seedlings in the experiments under consideration. A number of segmented glass tubes were set up in jars of freshly prepared agar and a wheat seedling placed in the upper end of each tube. When the agar had become partially solidified, air bubbles were produced by manipulating a glass tube in it. The bubbles were formed at the surface of the segmented tubes and at the level of the narrow openings. When the roots grew downward they showed the usual curvature at the openings. They did not, however, show any tendency to grow toward the air bubbles, nor to the agar in the vicinity of the air bubbles. Many roots grew directly through air bubbles and passed on without being deflected from their course by the presence of the air bubbles. It would be manifestly wrong to base judgment on this question if the roots passed from agar into air chambers and showed a tendency to remain there, since the environment would be changed in respects other than the air content. One might expect, however, that if an aerotropic tendency were manifested it might be shown by roots turning toward the agar in the vicinity of the air bubbles. Such a tendency was not manifested by roots in this or other experiments where air bubbles were present; hence it follows that the results reported are really due to a stimulation of the roots by some deleterious substance and not to a deficiency of oxygen.

PRELIMINARY EXPERIMENTS WITH OATS SEEDLINGS.

For comparison with the behavior of the roots of wheat seedlings a series of tubes was prepared which held oat plants. The segmented tubes contained and were surrounded by freshly prepared agar. The experiment lasted six days. The agar in the tubes became so toxic that 13 of the 39 roots employed were killed. Of the remaining 26 roots 19 curved and grew out of the tubes. This is a response of 73 per cent (the roots killed were not considered), and shows that the roots of oat seedlings produced a toxic condition which was quite repellent to themselves. In all cases it was the later roots which were killed; those which grew out into the surrounding fresh agar showed no signs of injury.

EXPERIMENTS IN WHICH MALIC ACID WAS ADDED TO THE CULTURE MEDIUM.

Continuous observation of the agar in which plants were grown spoke against the action of bacteria as a partial factor in producing the results. Nevertheless it was thought profitable to make an experiment in which bacteria were excluded.

After some preliminary experiments which showed that wheat

seedlings could tolerate malic acid, a quantity of wheat seedlings were grown in agar which contained 125 parts of malic acid per million. While this amount of acid was not sufficient to inhibit the growth of wheat roots, it reddened litmus paper instantly, and it is safe to assume that bacteria did not develop in such preparations. This experiment was so designed that the agar containing the malic acid, in which wheat seedlings had grown, was tested against freshly prepared agar, the segmented glass tubes being filled with one and surrounded by the other, i. e., part of the segmented tubes contained this agar in which a crop of seedlings had grown and were surrounded by fresh agar and the other segmented tubes contained the fresh agar and were surrounded by the used agar. This procedure will be described more in detail on page 31. The cultures were rotated to eliminate the action of gravity, as described in the following section.

Fifteen roots grew in segmented tubes containing fresh agar and surrounded by used agar; i. e., agar in which a crop of seedlings had previously grown. Of this number only four roots grew out into the used agar—a response of 27 per cent. Thirty-three roots grew in segmented tubes containing the used agar and surrounded by freshly prepared agar. Sixteen of these roots curved and grew out of the tubes into the freshly prepared agar—a response of 48 per cent. These figures are very similar and lead to the same conclusion as given by the similar experiments on page 32, where no precautions were taken to exclude bacteria. These results are taken to indicate that the growth of roots in agar, as described in the experiments, is not due to bacterial action. Another fact which overthrows such an objection is the consistent behavior of the wheat roots when wheat succeeded any given crop. It will be shown, for example, that agar in which wheat plants had previously grown had a deleterious effect when wheat roots were again planted in it. But when they were planted in agar in which cowpeas or corn had previously grown the deleterious effects were lacking. The chances for bacterial action were equally good in the cases of cowpeas or corn as they were in the case of the wheat. It becomes obvious, then, that the different behavior of the wheat roots in these different agars must be regarded as further evidence that the results described above and elsewhere are not due to the action of micro-organisms. It is quite possible that more extended experimentation would show that the behavior of the roots would be slightly modified when certain bacteria were present, but for the purpose of the present experiments they may be disregarded, although this method of experimentation would seem to be applicable to the study of many bacterial problems connected with soils and the roots of growing plants.

EXPERIMENTS IN WHICH THE ATTRACTIVE EFFECT OF GRAVITY ON THE ROOTS WAS NEUTRALIZED.

It is evident to anyone familiar with the growth of roots that the positive geotropism, or tendency to grow downward, inherent in the wheat roots would hinder their lateral curvature and growth out of the tubes, due to the stimulus of chemotropism.. The responses which have been thus far obtained are therefore the resultant responses of these two stimuli. One might expect that a root which was only feebly stimulated by the presence of the deleterious substances might be more strongly stimulated to grow downward by the attractive force of gravity, and hence show no response. The action of gravity can not be eliminated, but it can be neutralized by revolving the plants so that all sides are equally stimulated. In this and all following experiments the segmented glass tubes were placed in glass vials 5 cm. long and 2.5 cm. in diameter. These vials, wrapped in black paper and containing the tubes set in hardened agar, were attached to the arms of a dial driven by a small electric motor. The dial which supported the arms in this apparatus, known as a klinostat,[a] was 25 cm. in diameter and revolved once in two minutes.

The vials were attached to the arms of the klinostat in such a way that they revolved in a plane perpendicular to their long axes. One wheat seedling was placed in each segmented tube and each experiment lasted several days.

Three experiments were performed using freshly prepared agar. Out of a total of 47 roots, 31 curved and grew out of the segmented tubes, a response of 66 per cent. The response in similar tubes which had not been rotated had been 53 per cent.

Summing up the results of these experiments, it appears that the roots of wheat seedlings are repelled by some deleterious substance or substances produced during growth and that a satisfactory means of demonstrating the same is by the use of segmented glass tubes. Evidence is displayed to show that the curvature of the roots is not due to the action of light, of gravity, of water, nor to a lack of oxygen. Since the medium employed as a soil is as nearly as possible nonnutritive, the question of plant nutrients does not complicate the study. When the effect of gravity is neutralized a larger proportion of roots respond to the stimulus produced by the presence of toxic excreta.

EXPERIMENTS SHOWING THE BEHAVIOR OF WHEAT PLANTS GROWING IN A MEDIUM CONTAINING THE EXCRETA FROM THE ROOTS OF WHEAT OR OTHER PLANTS.

With the foregoing results in hand, the next problem was to study the behavior of one plant in the presence of excreta from various

[a] See Reed, Jour. App. Micros. and Lab. Methods, 6, 2269. 1903.

other plants. Wheat was selected as the plant to be employed as an indicator, since the roots which it puts out after the short life of the primary root are positively geotropic and sufficiently sensitive for chemotropic reactions.

It was shown in the preliminary experiments that the toxic effects remained in the agar in which plants had grown. It was also shown that the toxic effects persisted when such agar was melted and used again. In the experiments which are next to be described the effect of root excretions from wheat, corn, cowpeas, and oats were studied. The agar containing their excretions was obtained in each case by planting a large number of seedlings in a dish of soft agar and allowing them to grow for eight to fifteen days, according to the kind of plant employed. In a few days the agar was completely permeated by the roots of the plants, the plants being nourished in the meantime by the reserve materials of the seed. When the agar was to be used for an experiment the plants were pulled out, removing as little agar as possible. The agar was then placed in a shallow covered dish on the steam bath, stirred, and heated to a point between 70° and 85° C.

Continued heating at a high temperature changes or destroys the toxic substances. Even at this temperature some of the toxic effect was probably lost; hence unnecessary heating was avoided. As soon as the agar was completely melted it was filtered through absorbent cotton into the desired receptacles and cooled to room temperature. Distilled water was added to restore that lost by evaporation during the heating process.

The following series of experiments were so designed that the used agar was tested against freshly prepared agar, the segmented glass tubes being filled with one and surrounded by the other. The mode of procedure was as follows: Clean segmented tubes were placed in a jar of liquid agar, and at the proper time a seedling was placed in the mouth of each tube. When the agar had hardened throughout the entire jar, the tubes could be removed without disturbing the seedling or losing any agar from the tubes. The tubes were transferred to vials containing the other sort of agar which had cooled to a temperature between 30° and 38° C. When this agar was completely hardened, the vials were wrapped in black paper and put upon the klinostat. The quantity of agar in which plants had grown was always divided into two portions, one of which was used *inside* a set of tubes and the other portion *outside* another set of tubes. This procedure allowed of checking the results against each other. Thus the experiments designated under each heading as *a* constitute a check against those designated *b*, and vice versa.

All of the following results were obtained by rotating the cultures on a klinostat, as described above, to neutralize the effect of gravity.

WHEAT SUCCEEDING WHEAT.

(*a*) *Wheat plants in tubes of fresh agar, surrounded by agar in which wheat had been grown.*—The used agar was obtained and prepared in the manner outlined above. Five experiments were conducted comprising 89 roots. The details are given in the accompanying table.

Experiment.	Roots capable of responding.	Roots which grew out of tubes.	Per cent response.
1	8	0	0
2	22	12	55
3	12	2	16
4	32	13	40
5	15	4	26

Average response for the 5 samples of agar, 27 per cent.

It will be noted that only 27 per cent of the roots which grew as far as to the first opening in the tube turned and grew out into the surrounding agar, in which wheat plants had previously grown, as against 66 per cent when fresh agar was also used on the outside as in the experiment already described.

(*b*) *Wheat plants in tubes of agar in which wheat had been grown, surrounded by fresh agar.*—The results of six experiments are presented, showing that 62 per cent of the roots capable of responding grew out of the tubes containing the agar in which a previous wheat crop had grown into the fresh agar surrounding the segmented tube.

Experiment.	Roots capable of responding.	Roots which grew out of tubes.	Per cent response.
1	8	7	87
2	13	4	30
3	11	6	55
4	8	6	75
5	33	16	50
6[a]	41	30	75

Average response for the 6 samples of agar, 62 per cent.

It will be noted that the percentage of diverted roots in the several experiments varies somewhat. This is due to the varying toxicity of the used agar prepared at different times by the growth of different crops of wheat seedlings, as is shown by the fact that the differences are consistent in the two series, namely, that a high result in series *a* is always accompanied by a low result in series *b*, and vice versa for the same sample of used agar.

In the development of roots and tops the plants in series *b* usually excelled. This is probably due to the greater total quantity of fresh agar in that set. As soon as the roots passed out of the segmented

[a] Experiment 6 has no corresponding experiment in table *a* of this series.

tubes they were in a medium containing a relatively small amount of toxic excreta. It is obvious that toxic substances remain in the used agar and exert an influence on the succeeding crop. When the roots growing in freshly prepared agar reached the openings in the segmented tubes 27 per cent of them grew out into the used agar, whereas under the opposite set of conditions 62 per cent of the roots grew out of the tubes, the proportion of the responses being 44 : 100. This plainly indicates that there is some toxic substance in the agar which had grown a crop, the only source of which could be the excreta from the roots of the previous crop.

WHEAT SUCCEEDING CORN.

The corn used in these experiments was a variety of popcorn. When the seedlings had attained a length of 5 cm. they were planted thickly in dishes of soft agar. At the expiration of ten to fifteen days the seedling plants were removed and the agar melted for experiments in the manner previously described.

(*a*) *Wheat plants in tubes of fresh agar, surrounded by agar in which corn had grown.*—The accompanying table summarizes the results of 4 experiments. As much as 59 per cent of the wheat roots capable of response curved out and grew out of the tubes away from their own excreta into the agar containing the excreta of the previous corn crop.

Experiment.	Roots capable of responding.	Roots which grew out of tubes.	Per cent response.
1	13	7	54
2	20	10	50
3	13	9	70
4	28	17	61

Average response for the 4 samples of agar, 59 per cent.

(*b*) *Wheat plants in tubes of agar in which corn had been grown, surrounded by fresh agar.*—Four experiments were likewise performed in this series. Here as much as 62 per cent of the roots curved and grew out of the tubes. The details are shown in tabular form.

Experiment.	Roots capable of responding.	Roots which grew out of tubes.	Per cent response.
1	24	16	67
2	32	18	56
3	39	27	70
4	9	5	55

Average response for the 4 samples of agar, 62 per cent.

These results, obtained from the use of agar in which popcorn had previously grown, show that such agar is decidedly less toxic

to wheat than the agar in which wheat had grown. In all cases where popcorn agar was used a high per cent of roots curved and grew out of the tubes. The figures obtained (59 and 62 per cent) stand notably near that obtained when only freshly-prepared agar was employed, namely, 66 per cent. The percentages obtained in series *a* and *b* are in the proportion of 95:100. This means that the roots behave nearly the same, whether the tubes are surrounded by fresh or used agar, and that the toxic effect of the agar in which corn has grown is small, and is in fact nearly as good as if freshly-prepared agar had been used.

WHEAT SUCCEEDING COWPEAS.

The same method of procedure was followed as in the previous experiments.

(*a*) *Wheat plants in tubes of fresh agar, surrounded by agar in which cowpeas had grown.*—The results of 4 experiments employing 82 roots are tabulated.

Experiment.	Roots capable of responding.	Roots which grew out of tubes.	Per cent response.
1	12	8	67
2	38	21	55
3	23	9	39
4	9	6	67

Average response for the 4 samples of agar, 57 per cent.

(*b*) *Wheat plants in tubes of agar in which cowpeas had grown, surrounded by fresh agar.*—The 4 experiments corresponding to the above employed a total of 96 roots. The details are here given in tabular form.

Experiment.	Roots capable of responding.	Roots which grew out of tubes.	Per cent response.
1	20	11	55
2	31	23	74
3	26	17	65
4	19	11	58

Average response for the 4 samples of agar, 63 per cent.

The results of these two sets of experiments are closely similar to the preceding experiments, which employed agar in which corn had grown. That is to say, it makes little difference, so far as this response is concerned, whether the used agar is outside or inside of the segmented tubes. The results in the experiments with cowpeas are in the proportion of 90:100. This is interpreted to mean that

the excreta of the cowpea roots are very slightly toxic to roots of wheat seedlings.

WHEAT SUCCEEDING OATS.

The results of the preceding experiments point quite distinctly to the conclusion that the waste products of some plants are only slightly toxic to wheat seedlings. It seemed desirable to test oats, a more closely related species to wheat than either of the other two tested and one which in agricultural rotation is a bad crop to precede wheat.

Oats seedlings were allowed to grow in nonnutrient agar for eight to ten days, which was then melted for use as in preceding experiments.

(*a*) *Wheat plants in tubes of fresh agar, surrounded by agar in which oats had grown.*—The accompanying table shows the results of 4 experiments comprising 87 roots.

Experiment.	Roots capable of responding.	Roots which grew out of tubes.	Per cent response.
1	21	11	52
2	34	19	56
3	15	6	40
4	17	8	47

Average response for the 4 samples of agar, 47 per cent.

It will be noticed that only 47 per cent of the roots grew out of the tubes containing fresh agar into the oats agar.

(*b*) *Wheat plants in tubes of agar in which oats had grown, surrounded by fresh agar.*—The following table gives the results of 4 experiments which are complements of those given under *a*:

Experiment.	Roots capable of responding.	Roots which grew out of tubes.	Per cent response.
1	24	16	67
2	21	13	62
3	45	23	51
4	19	12	63

Average response for the 4 samples of agar, 61 per cent.

The results of these experiments show that the agar in which oats had grown was more toxic to wheat than that in which corn or cowpeas had grown. The proportion of roots which left the tubes in experiments *a* and *b* was 77:100, showing that there was a sensible difference whether the used agar was within or without the tubes. In the case of corn and cowpeas the proportions were 95:100 and

90:100, respectively, showing that there was only a slight difference whether the agar was within or without the tubes. From these relations we may conclude that the excreta of oats are more toxic to the roots of wheat seedlings than those of corn or cowpeas—a conclusion which is substantiated by the results obtained in crop rotation.

If we represent the relative responses of the roots in the *a* and *b* tests in the different experiments in the form of percentages, we obtain the following:

	Per cent.
Wheat succeeding wheat	44
Wheat succeeding oats	77
Wheat succeeding corn	95
Wheat succeeding cowpeas	90

Summing up the results of these experiments, which demonstrate the effect of root excreta from various sources upon wheat roots, it may be noted: (1) That the excreta from no other roots were so deleterious to wheat as its own excreta: (2) that the excreta from oats were more harmful than those from the more distantly related plants, cowpeas and corn: (3) that the plants which succeed best in a rotation of crops with wheat produce excreta which are least harmful to wheat.

While undue weight ought not to be given to these facts, it is undoubtedly true that they are of distinct significance in the principles and practice of crop rotation. That the roots of growing plants give off excretions has long been suspected, but it is only recently that any data have been obtained to show that such excretions may have a harmful effect upon the roots of succeeding crops.

THE RÔLE OF TOXIC EXCRETA IN THE GROWTH OF VEGETATION.

The existence of toxic excreta such as have been pointed out in this paper sheds light upon some phenomena not hitherto well understood.

Natural successions of plants have long been known. The students of plant distribution have given them careful study from the times of Humboldt and De Candolle. Although many factors determine the successions of vegetation, the accumulation of toxic excreta in the soil may be regarded as a factor of importance. This may possibly be the reason that a soil becomes in time less suitable for the growth of its native vegetation than for adventitious plants from another region.

The experiments which demonstrated the hostility of tree roots to wheat indicate that the action of the root excreta plays a part in determining the association of plants. The same indication is afforded by the Woburn experiments on fruit trees and the observations of Jones and Morse on butternut trees and of Hedrick on peach trees, as already described.

Another illustration of the antagonistic action of one plant upon another may be found in the "oak openings." These characteristic grassy tracts existed in the natural oak forests of Ohio, Indiana, and southern Michigan before they were modified by man. From some hitherto unexplained cause the forest was apparently unable to advance into these small prairies. In assuming that the grasses produced some substances which were unfavorable to the roots of trees, we have a factor which possibly has importance in the maintenance of such natural societies.

The curiously regular growth of "fairy rings" in a continually widening circle is probably due to the production of toxic excreta by the growing fungus. The young mycelium grows best on the outside of the ring because it is less affected by the excreta left in the soil within the ring. The common explanation for the development of fairy rings is based upon the assumption that the soil within the ring is so depleted of nutrients that it is unable to support the growth. An investigation of the chemistry of fairy rings by Lawes and Gilbert[a] showed such slight differences between the inside and the outside of the ring that this difference can not explain the entire absence of fungi within the ring. The total nitrogen outside of the rings (average of five rings) was 0.281 per cent; inside of the rings it was 0.247 per cent, a difference of 0.034 per cent. The average carbon outside the rings was 3.30 per cent; inside the rings, 2.78 per cent, a difference of 0.52 per cent. With our present knowledge of the ability of plants to absorb and utilize nutrients, these slight differences are utterly insufficient to explain the entire absence of fungi within the ring. The existence of toxic excreta in the soil would, however, explain it. It is of interest to note that such an explanation of fairy rings was suggested by Way.[b] This investigator admitted that "by far the most scientific and intelligible solution of the question is that which was based upon De Candolle's theory of the excretions of plants;" but on account of objections which appeared insuperable to him he was unable to accept it as a satisfactory explanation.

It has been previously mentioned that De Candolle[c] advanced a theory of crop rotation based upon this idea of excretions. He supposed that the excretions represented vegetable waste products, and argued that their presence in the soil would be as injurious to the plant as the excrement of an animal when presented to it as food. On the other hand, by change of crops other plants may profit by the excretions of its predecessors, absorbing them as food.[d] De Candolle

[a] Journ. Linn. Soc., **15**, 17, 1875; Journ. Chem. Soc., **44**, 3, 1883.

[b] Journal of the Royal Agricultural Society, **7**, 549, 1847.

[c] Physiologie vegetale. 1832. T. III, p. 1474.

[d] See also Boussingault, Rural Economy, trans. by Law, 1845, p. 345.

and his contemporaries failed to appreciate the agencies which effect the destruction of such organic substances in the soil, and maintained that once a crop had been grown the soil should be ever after toxic to that crop. Oxidation, brought about by proper cultivation, the action of micro-organisms in the soil, as well as the oxidizing power of the roots themselves, are important factors in destroying these deleterious bodies. In this work the action of substances ordinarily regarded as fertilizers also play a not insignificant part.

Liebig at one time supported De Candolle's theory of crop rotation, as is shown by the following statement, quoted from Gilbert:[a]

> The first definite theory as to the benefits of the alternation of crops assumed that the excreted matters of one description of crop were injurious to plants of the same description, but that they were not so, and might even be beneficial to other kinds of plants.
>
> At first Liebig pronounced this theory of rotation to be the only one having a really scientific basis. Later he seems to have modified his view considerably, and to have supposed that the explanation was, not that the excreted matters of one description of plant were injurious to another of the same description, but that as the different plants had such very different mineral requirements the alternation of one kind with another relieved the soil from exhaustion.

Under the domination of Liebig's theory of mineral requirements the theory of De Candolle was given up, the organic biological factors connected with plant growth were almost entirely neglected so far as agricultural investigations are concerned, and the purely mineral matter of both soil and plant claimed paramount attention. In an article entitled "On the Causes of Fertility or Barrenness of Soils,"[b] by John Coleman, presented in 1855 before the Royal Agricultural Society of England and awarded the prize of that association, the author says:

> The causes which operate in producing the fertility or barrenness of soils have hitherto to a great extent been shrouded in mystery, not from any want of study, but owing to the difficulties which meet the inquirer at every step, and the fact that most important results frequently depend upon causes which have eluded the search of the experimenter. The science of chemistry it was hoped would afford the key wherewith to unlock the mysteries of nature, but though its discoveries have conferred much practical benefit on the agriculturist, it has up to a very recent period effected comparatively little toward settling the causes of fertility or sterility. The theories of scientific men led us to expect that fertility depended upon the presence of certain mineral substances which were found invariably present in the ashes of plants, and the analysis of a soil it was believed would confirm the practical experience of the farmer; these hopes have been falsified except in the few cases of almost simple soils, such as pure clays and sands. In all other instances the analysis presented the existence in varying proportions of those substances supposed to induce fertility

[a] Agricultural investigations at Rothamsted, England, during a period of 50 years, p. 174. Bul. No. 22, Office of Experiment Stations, U. S. Department of Agriculture.

[b] Royal Agr. Soc. Jour., 16, 169 (1855).

equally in the barren as the fertile soil. The proportion of the various ingredients was next proposed as a sign of quality, but researches into the amount of inorganic matter abstracted by each crop have demonstrated that soils of a mixed character contain abundant supplies of mineral food for numerous crops.

This was fifty years ago, and the statements made are practically as true to-day as they were then. There has been a marked advance in agricultural practice, but until quite recently comparatively little light has been shed upon the scientific principles which underlie these practices. Agriculture has not shared in the great impulses which modern science has given to other arts and industries, and the domination of the mineral requirement theory proposed in the first half of the last century and accepted without adequate proof of its validity is largely responsible for the lack of development in agriculture commensurate with the enormous strides of other arts and industries under the guidance of modern scientific thought and research.

It is, perhaps, needless to say that the facts under discussion in this bulletin should be regarded primarily as placing certain agricultural practices upon a more rational basis.

When the majority of soils are kept in what is ordinarily known as "good tilth" by cultivation and continued rotation of crops, it is not probable that toxic root excretions will accumulate to an extent which would be harmful. But when one crop succeeds another of the same kind, these excretions may not be destroyed as rapidly as the best conditions for growth require. Especially is this the case if the soil is in a poor physical condition, unusually wet or dry, poor in organic matter, etc. From experiments related here and in the bulletins previously quoted, it appears that the substances in soil extracts having a toxic action are removed or destroyed by comparatively simple treatments. These experiments lend support to the fact that proper aeration of the soil will do much to destroy these organic substances which exert toxic effects. It is certain that the aeration would favor the decay of organic matter by promoting the activities of soil organisms and the processes of oxidation. The experiments which demonstrated the beneficial action of pyrogallol, of stable manure, and of green manure indicate furthermore that these organic substances may have a very specific action upon deleterious products arising from the growth of plants. It has been found, in fact, that the organic constituents of stable manure are more potent in overcoming the toxic action of an unproductive soil extract than all the inorganic plant food constituents[a] of the manure.

The fact is significant that the yield of wheat is usually smaller when it follows a crop of oats than when it follows corn or cowpeas. The smallest yields, however, are usually obtained when wheat fol-

[a] Bul. 36, Bureau of Soils, U. S. Dept. of Agr.

lows wheat. In our present state of knowledge it would seem that we must regard the excreta of growing roots as one of the main causes of the low yields obtained in improper crop rotations.

In some types of soil, influenced perhaps by certain climatic environments, there appear to exist conditions which are unusually favorable to the rapid destruction of toxic excretions. Such soils, when planted year after year to the same crop may not only maintain their original productive powers, but even increase with continued cultivation.

From the facts presented in this bulletin, it is evident that the production of toxic excretions by the roots of plants is undoubtedly a factor of importance in soil fertility. Many experiments have demonstrated that the accumulation of these toxic excretions may temporarily impair the fertility of certain soils. The foregoing experiments have not only shown that infertility may be due to actual toxic conditions of the soil, but also that the toxic conditions may arise from the growth of vegetation. The data given are just as conclusive in showing that the infertility of the soils was not due to their poverty in plant foot constituents.